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THE BRAIN OF THE EMU *DROMAEUS NOVAEHOLLANDIAE*

II. ANATOMY OF THE PRINCIPAL NERVE CELL GANGLIA AND TRACTS¹

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INTRODUCTION

This contribution is to supplement a paper published recently (Cobb and Edinger, 1962) on the gross anatomy of the brain and pineal body of the emu. Microscopic serial sections¹ were made of the whole of one of these brains (#104), embedded in celloidin, and cut at 25 microns thickness. The sections were stained with cresyl violet for cell bodies and with Loyez modification and Weigert's stain for myelinated nerve fibers. Pieces of the other brain (#85) were cut for Golgi and Bielschowski stains, for axons and glia. The report here presented, however, is far from being a thorough description of the histology of the emu's brain; it is a description of the large neuronal divisions, the gray masses of nerve cells, and the conspicuous fiber tracts. This is to enable the reader to obtain a general picture of the distribution of the gray matter in ganglia, nuclei, and cortex, the relation of the main ganglia to each other, and their main connections by tracts. Such a picture may serve as a basis for comparing the general neuronal arrangement of the emu's brain with other avian brains. An attempt has been made to estimate the size of different ganglia, but because of shrinkage in fixation and embedding, the absolute volumes are difficult to measure. A comparison of the size of one ganglion to another in the same brain, however, is possible with reasonable accuracy. Such measurements have significance in relation to function (Cobb, 1964).

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THE CEREBRAL VENTRICLES

In order to understand the brain of any bird, one must get an understanding of how the ventricular spaces are arranged, because they have a special relation to the cortex and corticoid areas. The ventricles of the avian brain are unlike those of other vertebrates, and among birds vary in shape and size. The ventricular system is filled with fluid and extends from the olfactory bulb to the spinal cord. In much of its course it is narrow; in the cerebral hemispheres it is often only a potential space, moistening two layers of brain which lie one upon the other (see Fig. 9).

In the olfactory bulbs the size of the ventricle varies greatly, from a tiny ependymal slit in the single fused bulb of small passerine birds, such as *Passer* (house sparrow), to a large open chamber in *Diomedea* (albatross) which has big separate bulbs. In the emu the ventricle is distinct but not large (Figs. 2, 3). The ventricle of the olfactory bulb is directly connected with the lateral ventricle of the cerebral hemisphere. This lateral ventricle lies between septum and striatum with its long dimension vertical (Figs. 4, 7). As it spreads backward it becomes larger, and as the mid-sections of the brain are reached the ventricle is seen to extend more and more laterally over the striatum (Figs. 8, 9). Here it lies under a sheet of tissue composed anteriorly of dorsal hippocampus and parahippocampus (Fig. 7), and farther back of corticoid tissue of three kinds: parahippocampal, dorsolateral and periamygdalar (Figs. 8, 10). Thus, over approximately the caudal third of the emu's cerebral hemispheres, the ventricle is a narrow, potential space separating a sheet of supraventricular tissue from the main mass of the underlying ganglia. The relation to the *nucleus diffusus*, or wulst (Fig. 4) is important. In the emu the wulst is frontally placed so the ventricles remain largely medial and vertical until the wulst becomes smaller caudally and the vallecule flattens out (Figs. 4, 5). Farther back, the ventricle spreads widely to each side and around to the base, making a complete covering of the occipital pole of the hemisphere (Figs. 9, 10).

The two lateral ventricles join at the base of the hemisphere, forming the third ventricle. This is continuous with the single ventricular space of the midbrain (aqueduct) which is large with lateral out-pocketings into the big optic lobes (Fig. 11). Much of these lateral ventricles of the midbrain appears to be

merely potential spaces, but at their mesial portions, where they join the aqueduct, the lumen is distinctly patent. Below the level of the midbrain the fourth ventricle is seen, wide beneath the cerebellum and narrowing down to become covered with nervous tissue in the medulla near the spinal cord.

ANATOMY OF THE FOREBRAIN

In birds, the main mass of the forebrain is composed of large gray ganglia (the "striatum") with a relatively small corticoid part, and variable, but usually small olfactory bulbs. Strictly speaking, the striatum of higher mammals is composed of the more dorsal cerebral gray ganglia traversed by bands of white fibers. Many of these run to and from the neocortex, making the striped appearance that gave the area its name. Such a combination of gray and white matter develops of necessity wherever there are gray ganglia forming axonal connections with each other. The naming of these ganglia in mammals and birds, as if they were homologous structures, has led to no little misunderstanding (Table 1). Rose (1914) was wise enough to simply name his ganglia A, B, C, etc., and Kuhlenbeck (1938), relying on embryological evidence, developed a nomenclature for the cerebral ganglia of birds that largely disregarded mammalian analogies. His work has been substantiated and effectively used by Jones and Levi-Montalcini (1958). Kuhlenbeck's investigations show that the ganglia (he calls them "nuclei") of the avian cerebral hemisphere arise from four embryonic zones, dorsomedial and ventromedial (the larger olfactory part) and dorsolateral and ventrolateral (the striatal nuclei); the latter two form the main masses of the cerebral hemisphere. A conspicuous boundary, the lamina medullaris dorsalis (Fig. 6) separates the striatal nuclei into two divisions, the epibasalis nuclei and the basalis. This seems to be a basis for a more rational nomenclature than the one built up by Kappers *et al.* (1936) on the comparative neurology of living reptiles and birds. This nomenclature is, therefore, used in this paper in describing the forebrain. Karten and Hodos (1966) in their recent atlas of the pigeon's brain use a modified Kappers nomenclature with abbreviations, as shown in my Table I. In mentioning different parts of the striatum, I use Kuhlenbeck's names and put Karten and Hodos' abbreviations in parentheses; for example: nucleus epibasalis caudalis (A) is the archistriatum. (See Table I and Fig. 1, and the list of abbreviations.)

Table 1
COMPARISON OF DIFFERENT NOMENCLATURES OF AVIAN FOREBRAIN GANGLIA

	COBB this paper	KARLEN and HODOS 1966	ROSE 1914	HUBER and (ROSBY 1929	KUTHLENBECK 1938; JONES and LEVI-MONTALCINI 1958
n. intercalatus	HIS	A	n. intercalatus hypstriatus	n. intercalatus	n. epibasalis dorsalis pars superior
n. diffusus	HA	B	Hypstriatum accessorium	n. diffusus dorsalis	
n. diffusus*	HD	C	Hypstriatum dorsale	n. epibasalis dorsalis pars superior	
n. epibasalis dorsalis	HY	D	Hypstriatum ventrale	n. epibasalis dorsalis pars inferior	
n. epibasalis centralis	{ N / E	G	{ Neostriatum / Ectostriatum	n. epibasalis centralis	
n. epibasalis caudalis	A	K	Archistriatum	n. epibasalis caudalis	
n. basalis	PA	H	Paleostriatum augmentum	n. basalis	
n. entopeduncularis	PP	J	Paleostriatum primitivum	n. entopeduncularis	

* These three nuclei make up the wulst. In emu the *lamina frontalis* is not clearly divided into *suprema* and *superior* with a "hypostriatum dorsale" lying between. The nucleus intervalatus is not well defined and lies between the fibers of the lamina in a lateral position (see Fig. 4). Therefore, in describing emu the *n. diffusus* is not subdivided but is considered to be all the grey matter lying above or within the lamina frontalis.

Figure 1 is drawn from a reconstruction of the forebrain of the emu, the main ganglia or nuclei being shown in seven sections at the levels indicated by the vertical lines drawn on the lateral view of the whole brain (insert). The wulst or nucleus diffusus (HA, HD) is seen in five sections; beginning with the most anterior it is the largest; in the second and third it is large and then tapers off in the fourth and fifth. The largest nucleus of all, the nucleus epibasalis centralis (N and E), appears as a small part of the third section and enlarges caudally until it is the only ganglion present in the most caudal section. Other main nuclei can be similarly traced to show their antero-posterior relationships. The relation of one nucleus to another in any one section can be seen in the photographic reproduction

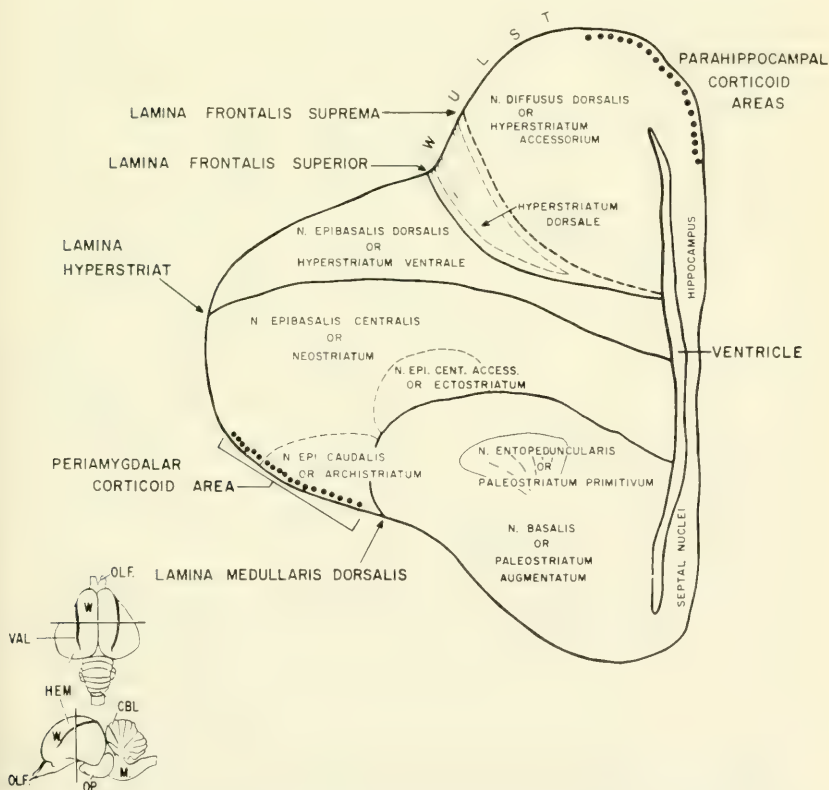


Fig. 1A. A diagrammatic representation of the dorsoventral relations of the principal forebrain ganglia, but no one section could show all of these.

of the sections that represent various levels (Figs. 2 to 11). The nucleus intercalatus is found in most birds. In the emu it is a rather inconspicuous part of the wulst lying between the fibers of the lamina frontalis (Fig. 4). It is composed of small nerve cells and is more compact than the rest of the nucleus diffusus of which it is a part (if the nucleus diffusus is defined, as in this paper, as that part of the gray mass lying within or above the lamina frontalis).

The division between wulst (nucleus diffusus) (HA, HD) and nucleus epibasalis dorsalis (HV) is quite clear in the emu, the lamina frontalis being well developed, but in my specimen it is not split into two parts, superior and suprema. Therefore, one cannot make out a distinct nucleus lying between the parts

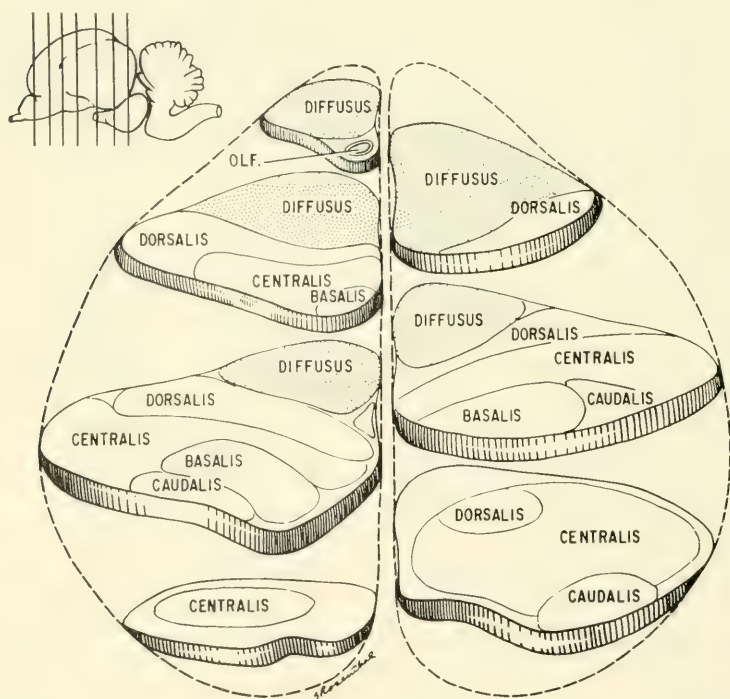


Fig. 1B. A simplified diagram of the principal forebrain ganglia showing perspective, to give some idea of the anteroposterior relationships. The serial sections from which the diagrams were drawn are (from front to back) #161, #361, #501, #701, #901, #1201, #1281. Their position on the whole brain is shown by vertical lines on the small inset.

of the lamina as described in some birds' brains. Rather, one sees a branching of the lamina frontalis with many cells lying in the interstices. Some of these are small and might be said to form a group which could be called nucleus intercalatus (Figs. 6, 7). This is not clear in sections farther forward (Fig. 4). In fact, no boundaries would seem to be definite enough to justify describing a distinct nucleus; in short, I do not find in emu a nucleus epibasalis dorsalis, pars superior (HD). Below the lamina frontalis the nucleus epibasalis dorsalis (HV) is well defined and bounded ventrally by the lamina hyperstriatica (Figs. 4, 6).

CORTEX AND CORTICOID AREAS

The question of the avian cerebral cortex (pallium) is complex and controversial. Craigie meticulously described the corticoid areas of the emu (1935 A, B). In the next year Kappers, Huber and Crosby (1936) modified Craigie's findings to some extent. Bures, Fifkova and Marsala (1960) have made a good summary of the "cortex question," but, unfortunately, their nomenclature differs from others. I am using the names of corticoid areas and hippocampus as used by Kappers, Huber and Crosby (1936) because they seem simpler and freer from implied homologies to mammalian brains.

In the emu there is a well developed archicortex, the hippocampus, with three or four obvious layers. These become less distinct in the dorsal hippocampus (Fig. 7), and lamination cannot be seen clearly at all in the parahippocampal corticoid areas which have a thin single or sometimes double layer of cells lying over the surface of the wulst. Further laterally, the dorsolateral corticoid area is even thinner and less distinct (Fig. 8). As one goes towards the posteroventral part of the hemisphere, a definite corticoid area with two layers of cells is seen over the nucleus epibasalis caudalis (A). This is called the periamygdaloid corticoid area (Fig. 8). Also ventral but far forward is seen another conspicuous corticoid area, the praepyriiform. It lies about the root of the olfactory bulb where it joins the frontal pole of the hemisphere (Fig. 3).

The relationship of these corticoid areas to the cerebral cortex of mammals is not well understood. The fiber connections of the parahippocampal areas suggest a function analogous to that of neocortex in mammals, but these areas are surely not homologous

with mammalian neocortex; their homology to the "general cortex" of reptiles is more clear. The area described by Goldby and Gamble (1957) as "dorsal cortex" seems to correspond with what is called here "parahippocampal corticoid," and called "general cortex" by Kappers, Huber and Crosby (1936). A thickening found in this "dorsal cortex," which overlies the anterior dorsal part of the striatum, occupies a position in the pallium from which, *in the embryo*, cortex is seen to develop. In such a topographical sense only can this cortex be said to be homologous with mammalian neocortex.

There is better evidence that the periamygdalar corticoid areas are homologous with the temporal mesocortex of mammals, and that the praepyriiform corticoid areas are homologous with the entorhinal areas of mammals. One thing seems sure, and that is that birds (including the emu) have no neocortex. For a scholarly and thorough discussion of this vexing question, the reader is referred to Kühlenbeck's recent book (1966).

COMPARATIVE MEASUREMENTS OF GANGLIA IN THE FOREBRAIN

Believing that increase of any function in an animal is positively correlated with increase in size of the parts of the brain significantly involved, it is of interest to compare the sizes of the different parts of the brains of birds of various families and varied types of behavior. This has been done in relation to the auditory nuclei (Winter, 1963), the olfactory bulbs (Cobb, 1960), auditory and visual centers of the midbrain (Cobb, 1964), and ganglia of the forebrain (Fritz, 1949). Since we know so little about the function of the different ganglia of the forebrain, it is difficult to choose which ganglia to measure. Fritz showed differences in size of the ganglia he measured, but no correlations with any functions. He chose to measure the volume of "hyperstriatum" (n. diffusus plus n. epibasalis dorsalis), "neostriatum" (n. epibasalis centralis), "archistriatum" (n. epibasalis caudalis), and "paleostriatum" (n. basalis plus n. entopeduncularis). The boundary between the neostriatum and archistriatum is not always clear, as pointed out by Fritz.

I decided to measure: 1) n. diffusus, both parts plus n. intercalatus (i.e. all the ganglionic mass above the lamina frontalis superior); 2) the n. epibasalis dorsalis (HV); 3) the n. epibasalis centralis (N, E). The first was chosen because it seemed, grossly, to vary so much from species to species, the

other two because they are large forebrain ganglia and are possibly associative in function and hence related to "higher integrations" and "intelligent" behavior (Table II).

In the brainstem the n. isthmi, n. mesencephalicus, and tectum opticum were chosen because of their relation to hearing and vision, as described in a previous paper (Cobb, 1964), and by Karten (1966). The method of estimating the volume of each of these ganglia and of the whole hemisphere, with which they are compared, has been described previously (Cobb, 1964). Briefly, it is to project and draw the structures to scale, and, by knowing the thickness of the sections and their distances apart and number, to compute the volume. Absolute values for volumes of different structures are not reliable because of differences in shrinkage from one brain to another, but relative measurements in any one series of slides made from one brain are significant.

An attempt was made to measure the areas of the hippocampus and the corticoid structures, but because of their long and narrow shapes, it was difficult to use the planimeter to measure their areas. Photographs were therefore made to scale and the desired areas were cut out of each print and weighed. By this method (Fritz, 1949), it was estimated that the n. diffusus (HA and HD) had a volume 28 per cent as large as the hemisphere, and that the hippocampus plus the corticoid areas had a volume 13 per cent of the size of the hemisphere. By the projection planimeter method (Cobb, 1964) the n. diffusus (HA and HD) was also found to be 28 per cent of the hemisphere. For these quantitative data on the emu brain see Table II.

Table II
VOLUMES OF CERTAIN PARTS OF EMU BRAIN

Volume of one cerebral hemisphere (before fixation) approximately 6.3 cc	
	<i>percentage of hemisphere</i>
Nucleus Diffusus (HA & HD)	28
N. Epibasalis Dorsalis (HV)	11
N. Epibasalis Centralis (N & E) ¹	32
Volume of one optic lobe (before fixation) approximately 0.5 cc	
	<i>percentage of optic lobe</i>
N. Mesencephalicus Lateralis	5.4
N. Isthmi Magnocellularis	1.9
N. Isthmi Parvocellularis	2.5
Tectum Opticum	81.0

¹ As defined in section on abbreviations and nomenclature and Fig. 1.

As to the compactness of the emu's brain, it is obvious by microscopic inspection that there are fewer nerve cell bodies (perikarya) in a given area than in the brains of smaller birds. Comparison was made by counting the number of cells in 0.0143 of a square millimeter in microscopic slides of brain tissue of the emu and of a hummingbird (*Selasphorus platycercus*). Knowing the thickness of the section, the number of cells per cubic millimeter was computed for stratum E of the optic tectum of the midbrain, and for the midposterior part of the n. epibasalis centralis (N). In each of these cases the emu was found to have less than half as many cells per cubic millimeter as the hummingbird (see Table III). Purkinje cells in the cerebellum were also counted and measured in these two birds, and the ratio of 1 to 2 was also approximated. Because of the linear arrangement of Purkinje cells along the edge of a stratum, cells per volume could not be counted, but cells per linear micron of the layer were easily figured. One should not lay too much claim to accuracy in these determinations of cells per given volume, because in the process of fixing and embedding in celloidin, there is much shrinkage of the brain tissue, and the amount of shrinkage in two separately prepared series of brain sections cannot be accurately estimated. In my series of brains it seems to be about 20 or 23 per cent of the volume of the fresh brain. The figures are given in tabular form, with emphasis on the fact that they are only approximate (Table III).

Table III
ESTIMATES OF COMPACTNESS OF EMU BRAIN
COMPARED TO HUMMINGBIRD

	<i>Dromaeus novae-hollandiae</i>	<i>Selasphorus platycercus</i>
Number of cells per mm ³ of n. epibasalis centralis (N).	42,800	125,000
Number of cells per mm ³ of stratum E of tectum	40,000	100,000
Purkinje cells per 100 linear micra	2.2	4.8
Average diameter of Purkinje cells	26.0 micra	12.0 micra

GRAY NUCLEI AND LAMINAE OF MIDBRAIN AND HINDBRAIN

Figures 8 to 12 show the main gray masses of the midbrain and hindbrain; these masses are either nuclei, large and small, or laminated structures such as the nerve cell layers of the tectum opticum and cerebellum. This laminate pattern has neurons oriented in three planes, the axons usually parallel and the dendrites and collaterals at right angles, making a criss-cross arrangement in which layers of cells are more or less clearly separated by layers of fibers. Such an arrangement of neurons probably is more plastic in function than the arrangement in nuclear masses, allowing more rapid and efficient adaptations to environmental change (Yakovlev, 1952). The acme of such development is seen in the mammalian cerebral neocortex. In birds, where vision is of such great importance, it is remarkable that a visual cortex has developed in the tectum of the midbrain, but none in the forebrain.

The cerebellum, in the hindbrain, is an example of an organ with laminated cortex, subserving rapid coordination in widespread neuronal integrations. The three-layered arrangement of neurons is uniform throughout the wide extent of this cortex (Fig. 12).

Sections were made of the pineal body, but were stained only with hematoxylin and eosin, so no refinements of histology could be identified. However, one could see the structures described by Quay (1965): a sac-like formation, tubules and follicles, and a mass of cellular parenchyma. In two areas there were conspicuous lymphoid nodules. In general, the histology of the pineal body is more like that of the Galliformes than the Passeriformes.

SUMMARY

The emu, like the ostrich, is an enormous running bird and cannot fly. This specimen weighed 31 kilograms. The brain of the emu is one of the largest avian brains, and less compact than the brains of smaller birds. The forebrain is well developed with medium sized hippocampus and parahippocampal corticoid areas. The size of these areas is probably related to the medium size of the olfactory bulbs. The gray nuclei that make up the forebrain are much like those of *Gallus* in arrangement and relative size, except for the nucleus diffusus (wulst or hyperstriatum

accessorium) which is relatively larger and is bounded below by a loosely arranged lamina frontalis. This cannot be divided into two parts, superior and suprema. The nucleus intercalatus is represented by a group of small cells in the lateral part of the area crossed by the sparse upper fibers of the lamina frontalis. Little is known about the function of the wulst. Its connections with the optic tectum of the midbrain indicate that it has something to do with vision, and the large size of the emu's eye suggests a reason for the big wulst.

The midbrain is remarkable for its large optic tectum with seven definite layers, but this visual cortex is conspicuous in all birds, the emu rating above the average of most birds in relative size of tectum, but not as high as the Falconidae. In the hindbrain there is nothing remarkable; the cerebellum is well developed but not relatively as large as in many birds with skill in flying.

REFERENCES

BÜRES, J., E. FIFKOVA and J. MARSALA

1960. Leao's spread in depression in pigeons. *J. Comp. Neurol.*, **114**:1.

COBB, S.

1960. A note on the size of the avian olfactory bulb. *Epilepsia*, **1**:394-402.

1964. A comparison of the size of an auditory nucleus (n. mesencephalicus lateralis, pars dorsalis) with the size of the optic lobe in 27 species of birds. *J. Comp. Neurol.*, **122**: 271-280.

COBB, S. and T. EDINGER

1962. The brain of the emu (*Dromaeus novae-hollandiae*, Lath) 1. Gross anatomy of the brain and pineal body. *Breviora, Mus. Comp. Zool. No.* **170**: 1-18.

CRAIGIE, E. H.

1935a. The hippocampal and parahippocampal cortex of the emu. *J. Comp. Neurol.*, **61**: 563.

1935b. The cerebral hemispheres of the kiwi and emu. *J. Anat.* **69**: 380-393.

FRITZ, W.

1949. Vergleichende Studien über den Anteil von Striatumteilen am Hemisphärenvolumen des Vogelhirns. *Rev. Suisse Zool.*, **56**: 461-491.

GOLDBY, F. and H. J. GAMBLE

1957. The reptilian cerebral hemispheres. *Biol. Rev.*, **32**: 383-420.

HUBER, C. G. and E. C. CROSBY

1929. The avian diencephalon. *J. Comp. Neurol.*, **48**: 1-177.

JONES, A. E. and R. LEVI-MONTALCINI

1958. Patterns of differentiation of the nerve centers and fiber tracts in the avian cerebral hemispheres. *Arch. Ital. Biol.*, **96**: 231-281.

KAPPERS, C. U. A., G. C. HUBER and E. C. CROSBY

1936. The comparative anatomy of the nervous system of vertebrates, including man. New York, MacMillan, 2 vols.

KARTEN, H. J. and W. HODOS

1966. Stereotaxic atlas of the pigeon's brain. (In press).

KUHLENBECK, H.

1938. The ontogenetic development and phylogenetic significance of the cortex telencephali in the chick. *J. Comp. Neurol.*, **69**: 273-295.

1966. Comparative anatomy of the vertebrate brain. (In press).

QUAY, W. B.

1965. Histological structure and cytology of the pineal organ in birds and mammals. *Progress in Brain Research*, **10**: 49-86.

ROSE, M.

1914. Ueber die cytoarchitektonische Gliederung des Vorderhirns der Vögel. *J. Psychol. Neurol.*, **21**: 278-352.

SMITH, G. E.

1919. A preliminary note on the morphology of the corpus striatum and the origin of the neopallium. *J. Anat.*, **53**: 271-291.

WINTER, P.

1963. Vergleichende qualitative und quantitative Untersuchungen an der Hörbahn von Vögeln. *Z. Morphol. Ökol. Tiere*, **52**: 365-400.

YAKOVLEV, P. I.

1952. Patterns of neuronal assemblies and the anatomical substratum of seizures. *Epilepsia*, (Ser. 3) **1**: 51-68.

ABBREVIATIONS AND NOMENCLATURE USED IN THE FIGURES

(See also Table I)

A. SEPTAL.	Area septalis
ANT. COM.	Anterior commissure, interconnects n. epi. caudales of the two hemispheres
ANT. MED. VEL.	Anterior medullary velum merges anteriorly with tectal commissure, which is the dorsal part of post. com.
CBL	Cerebellum. Its cortex has 4 layers: 1. molecular 2. Purkinje cells 3. granular 4. medullary
CENTR. GRAY	Central gray matter around ventricle

CHORIOID	Plexus chorioideus of the third ventricle
DORS. LAT. CORTICOID OR DORSOLAT. CORTICOID	Dorsolateral superficial corticoid area, anteriorly on surface of wulst, posteriorly outside the ventricle
FASC. LONG. POST.	Fasciculus longitudinalis posterior
HABENULA	An olfactory way station of epithalamus
HEM.	Cerebral hemisphere
HIPPOCAMP.	Hippocampus or cortex ammonialis
INNER GRAN.	Inner granular layer of cells.
LAM. FRONT.	Lamina frontalis. Sometimes separated into superioris and suprema
LAM. HYPERSTRIAT.	Lamina hyperstriatica
LAM. MEDUL. DORS. OR LAM. MED. DORS.	Lamina medullaris dorsalis
LAT. F. B. BUNDLE	Lateral forebrain bundle, contains tracts to thalamus, midbrain, and hindbrain
LAT. LEM.	Lateral lemniscus, lies in fibrous capsule of n. mesen. lat.
LAT. LEM., D.P.	Dorsal peduncle
LAT. LEM., V.P.	Ventral peduncle
LAT. VENT.	Lateral ventricle of the cerebral hemisphere
LAT. VENT. M.B.	Lateral out-pocketing of the midbrain ventricle beneath the tectum
M	Medulla oblongata
N. BASALIS	Paleostriatum augmentatum, the nucleus separated from neostriatum above and laterally by the lamina medullaris dorsalis; PA (Karten); Field H (Rose)
N. CEREBEL. LAT.	Nucleus cerebellaris lateralis
N. DIFF. DORS.	Nucleus diffusus dorsalis or hyperstriatum accessorium, HA (Karten), Field B (Rose)
N. DORSOLAT.	Dorsolateral nucleus of the thalamus
N. DORSOMED.	Dorsomedial nucleus of the thalamus
N. ENTOPED.	Nucleus entopeduncularis, or paleostriatum primitivum; PP (Karten); Field J (Rose)
N. EPI. CAUDALIS	Nucleus epibasalis centralis or archistriatum (amygdala); A (Karten); Field K (Rose)
N. EPI. CENTRALIS	Nucleus epibasalis centralis or neostriatum, the ganglion just below lamina hyperstriatica, N and E (Karten); Field G (Rose)
N. EPI. DORSALIS	Nucleus epibasalis dorsalis pars inferior or hyperstriatum ventrale, the ganglion lying just below the lamina frontalis; HV (Karten); Field D (Rose)
N. GENIC.	Nucleus geniculatus lateralis
N. HYPOTHAL.	Nucleus hypothalamicus

N. INTERCAL.	Nucleus intercalatus hyperstriaticus; HIS (Karten); Field A (Rose), of nucleus diffusus dorso-lateralis
N. INTERPED.	Nucleus interpeduncularis
N. ISTHMI	Nucleus isthmi, pars magnocellularis
N. MESEN. LAT.	Nucleus mesencephalicus lateralis, pars dorsalis, also called torus semicircularis
N. MESEN. PROF.	Nucleus mesencephalicus profundus or tegmento-pedunculopontinus
N. NERV. ABDUC.	Nucleus nervus abducentis
N. OCULOMOT.	Nucleus oculomotorius
N. OLIV. SUP.	Nucleus olivarius superior
N. OVOID.	Nucleus ovoidalis
N. PARAVENT.	Nucleus paraventricularis magnocellularis
N. PRETECT.	Nucleus pretectalis
N. ROTUNDUS	Nucleus rotundus
N. RUBER	Nucleus ruber or red nucleus
N. SPIRIFORM.	Nucleus spiriformis
N. SUBPRETECT.	Nucleus subpretectalis
N. VESTIB. LAT.	Nucleus vestibularis lateralis, Deiter's nucleus
N. VESTIB. VENTRO-LAT.	Nucleus vestibularis ventrolateralis
OLF.	Olfactory bulb
OLF. VENT.	Ventricle of olfactory bulb
OP.	Optic lobe
OP. CHIASM	Optic chiasm
OUTER GRAN.	Outer granular layer of cells
PARAHIP. CORTICOID	Parahippocampal corticoid areas
PERIAMYG. CORTICOID	Periamygdalar corticoid area, contiguous with the parahippocampal areas; not outside the ventricle
PONT. GRAY.	Pontine gray nuclei
POST. COM. OR P. COM.	Posterior commissure, from tectum to opposite tectum and also connects spiriform and dorsal mesencephalic nuclei
PREPYR. CORTICOID	Praepyriform corticoid area
STRAT. FIBR.	Stratum fibrosum
SUPRAOPTIC.	Dorsal supraoptic decussation
TECTUM OP.	Tectum opticum of the midbrain. Divided into six layers or strata (Huber & Crosby 1924) A. Stratum opticum B. Stratum fibrosum et griseum superficiale C. Stratum album centrale D. Stratum griseum centrale E. Stratum griseum periventriculare F. Stratum fibrosum periventriculare
TR. FRONTO-ARCHISTRIAT.	Tractus fronto-archistriaticus

TR. OCCIP.-MESEN.

Tractus occipito-mesencephalicus

TR. OP. MARG.

Tractus opticus marginalis, lamina A of the optic tectum. Input from optic nerve to tectum

TR. SEPTOMESEN.

Tractus septomesencephalicus

TR. THAL-STRIAT.

Tractus thalamo-striatalis

V. OR VAL.

Vallecula

VENT. M.B.

Midbrain ventricle or aqueduct of Sylvius

W.

Wulst



Fig. 2. Serial section #81. Olfactory bulbs, Cresyl Violet stain, magnification X 7.0.

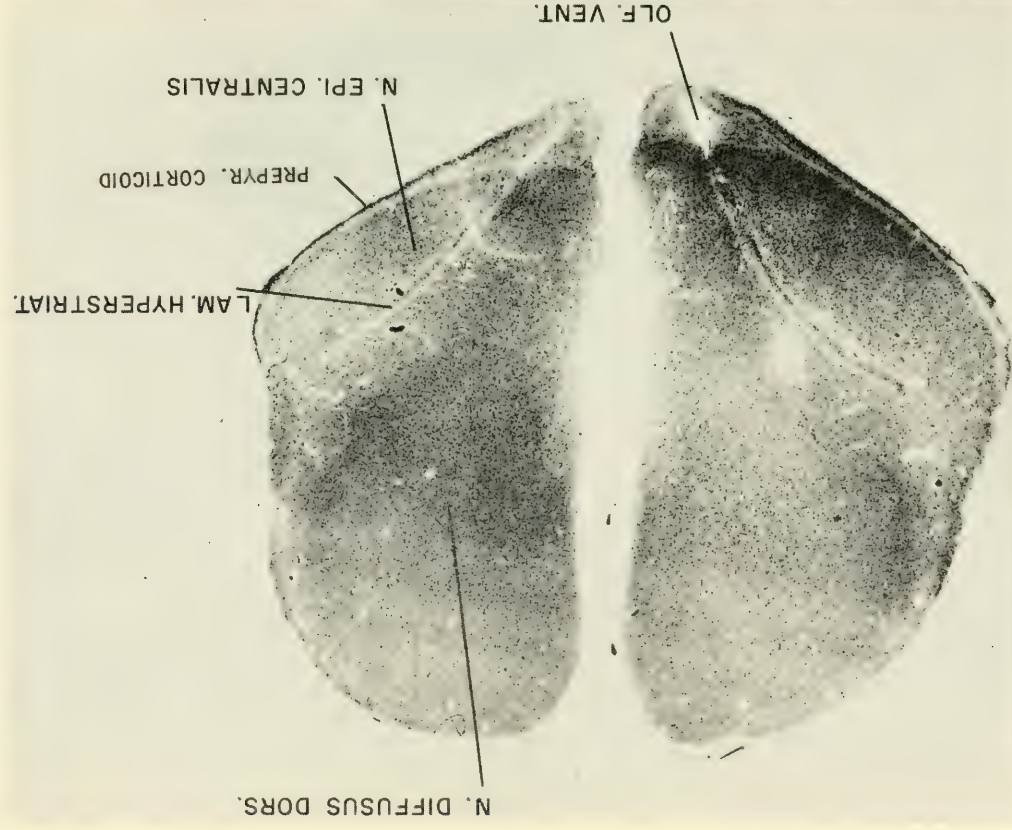


Fig. 3. Serial section #401. Cresyl Violet stain, magnification X 5.0.

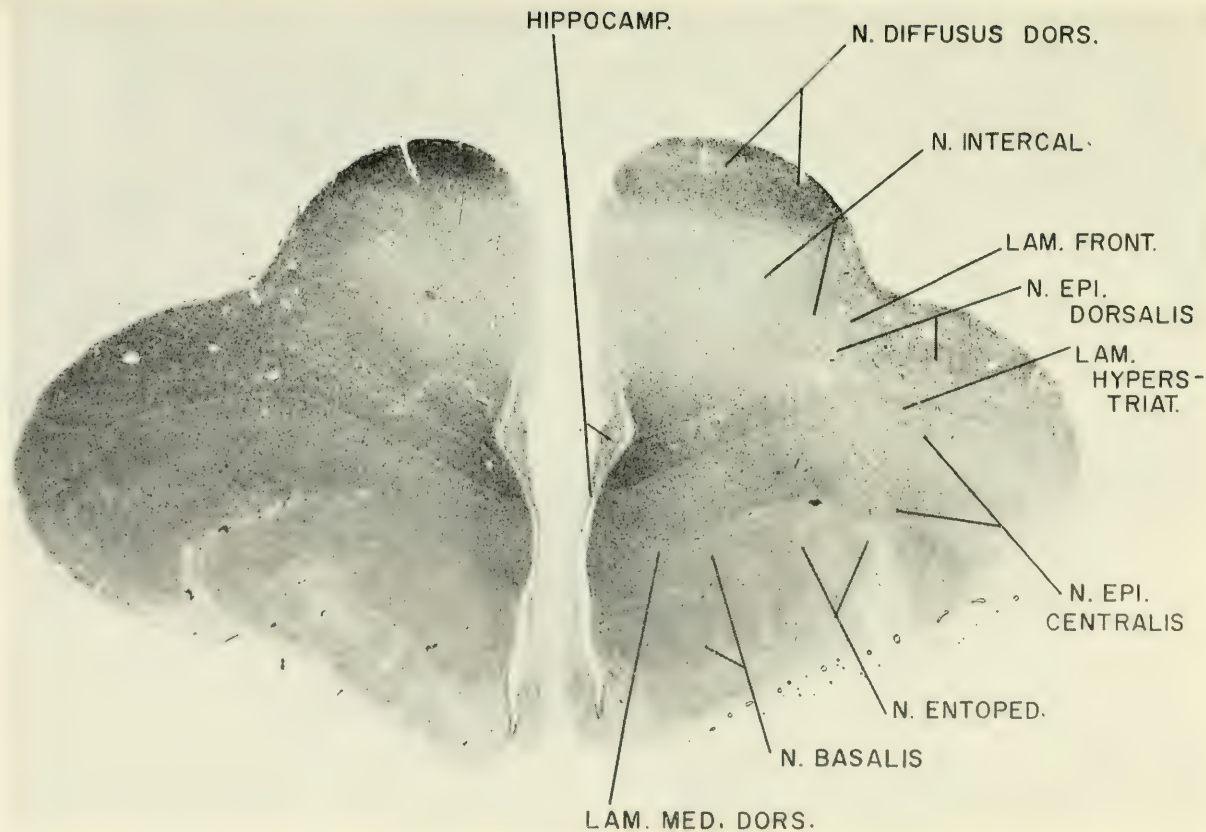


Fig. 4. Serial section #681. Cresyl Violet stain, magnification X 5.0.

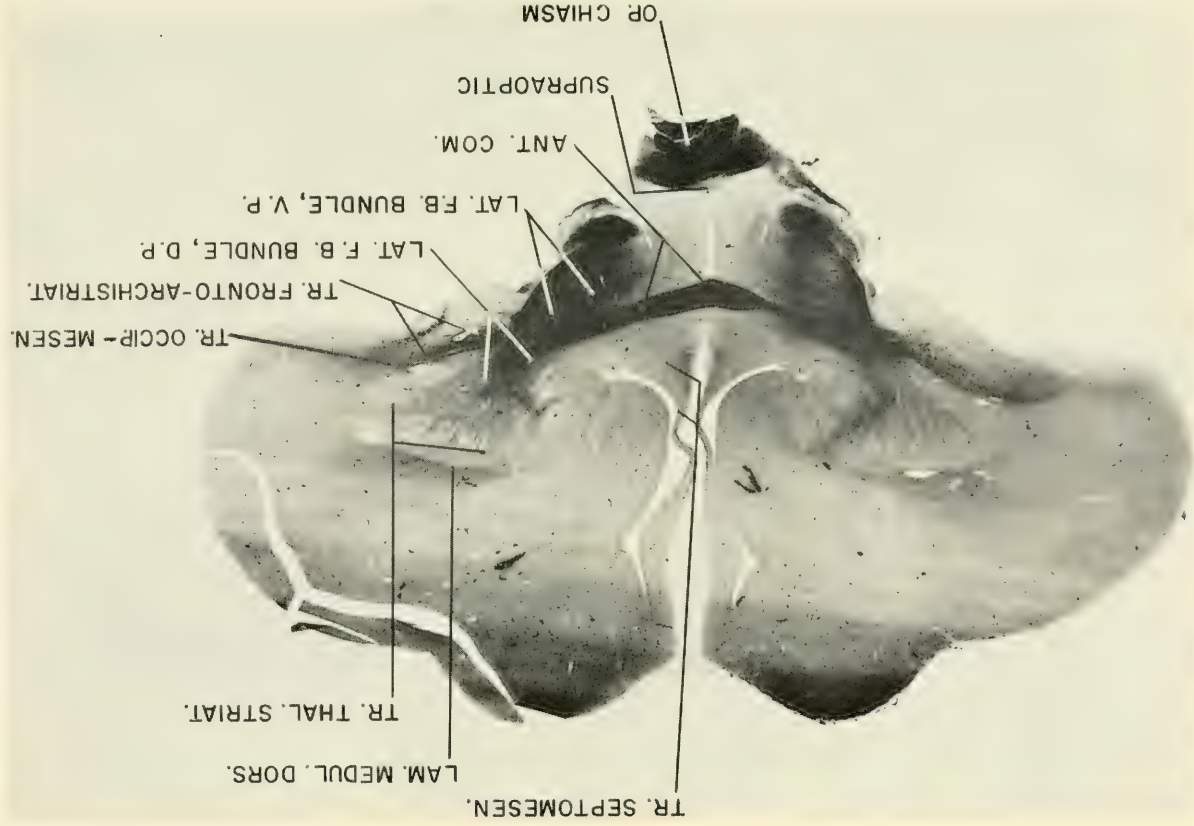


Fig. 5. Serial section #900. Loyez stain, magnification X 5.0.

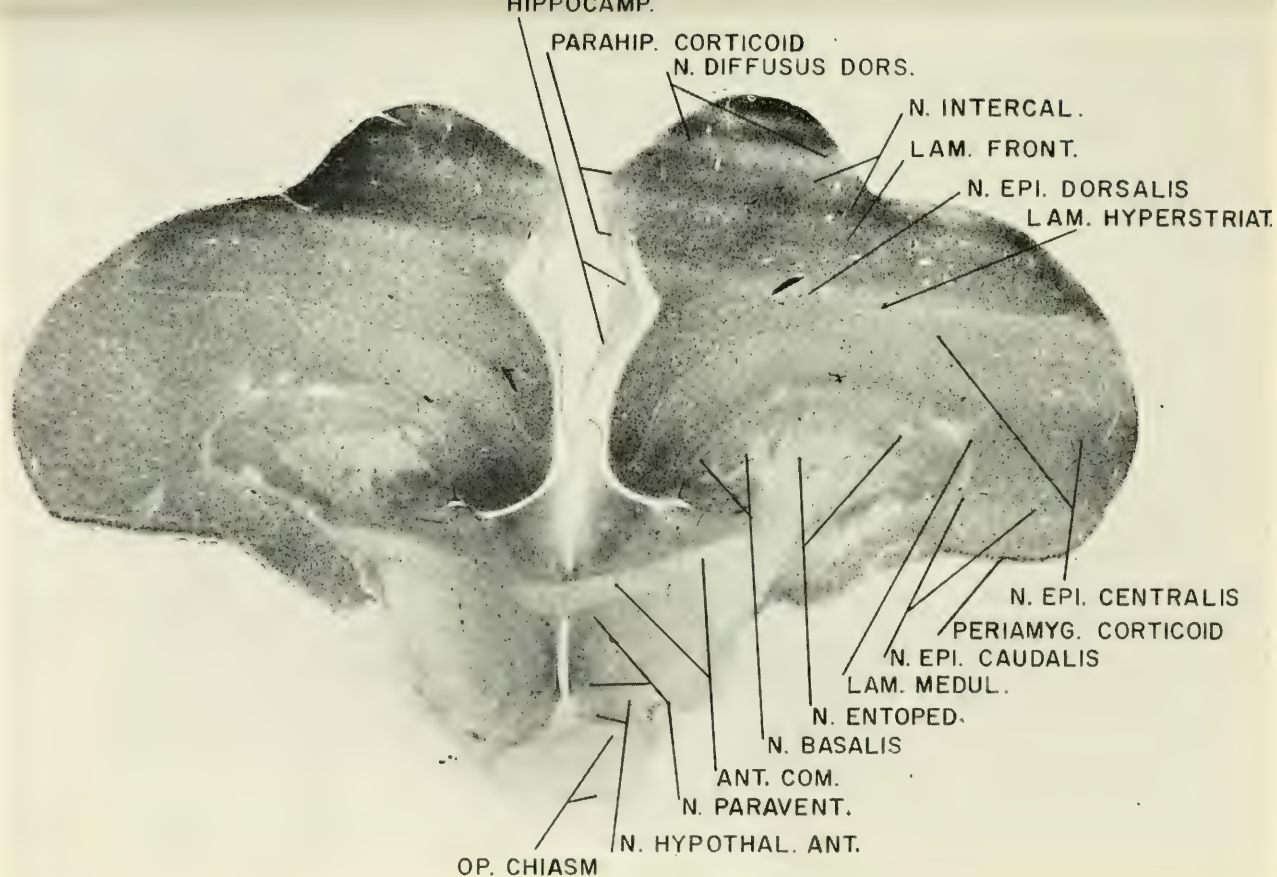


Fig. 6. Serial section #901. Cresyl Violet stain, magnification X 5.0.

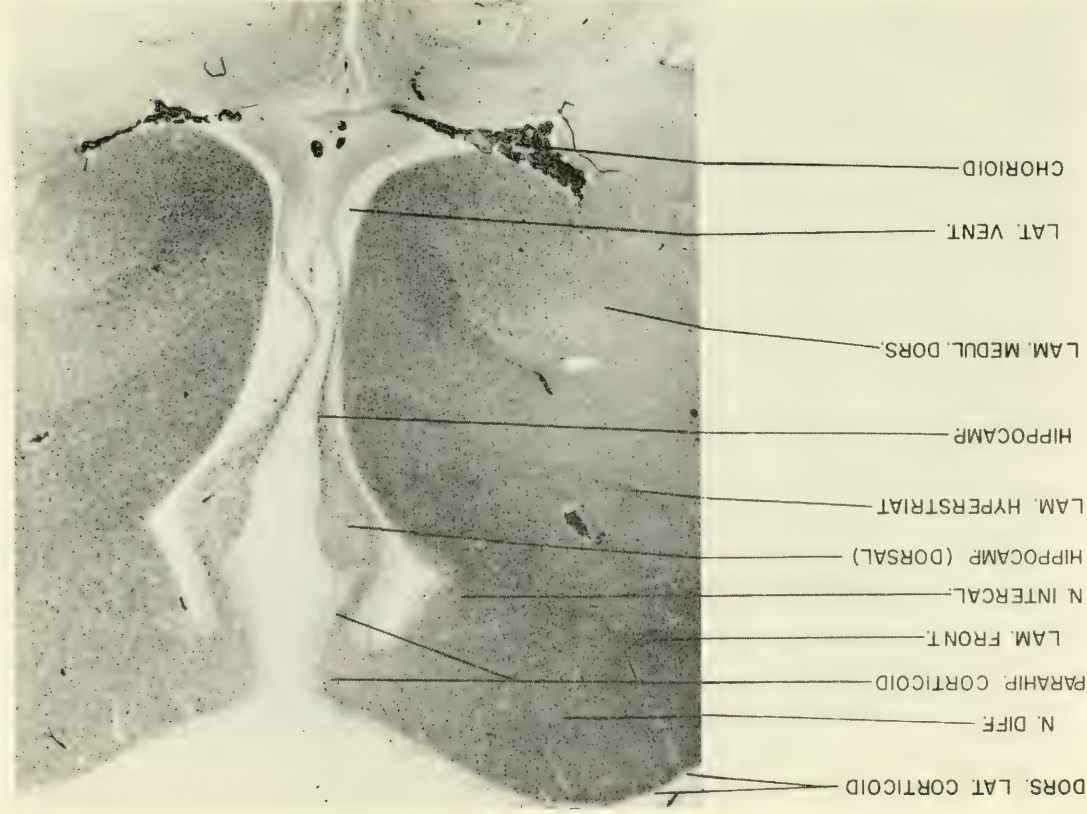
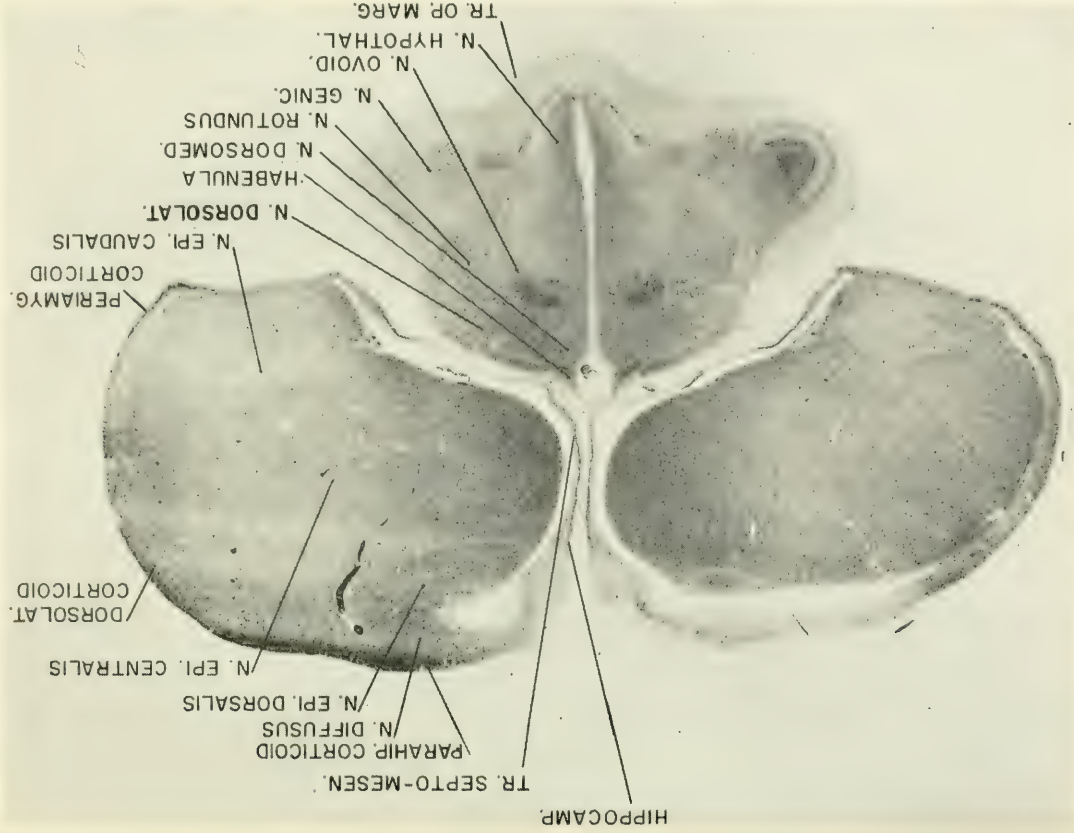


Fig. 7. Serial section #961. Cresyl Violet stain, magnification X 8.0.



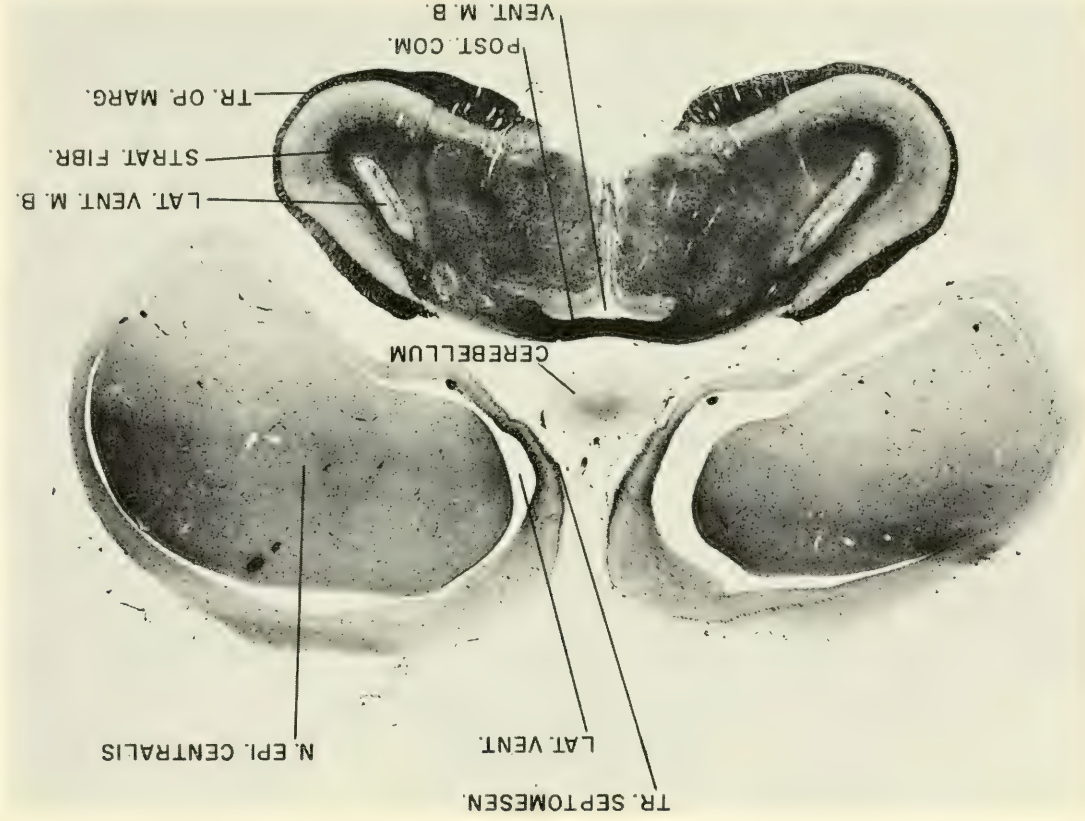


Fig. 9. Serial section #1200. Loyez stain, magnification X 5.0.

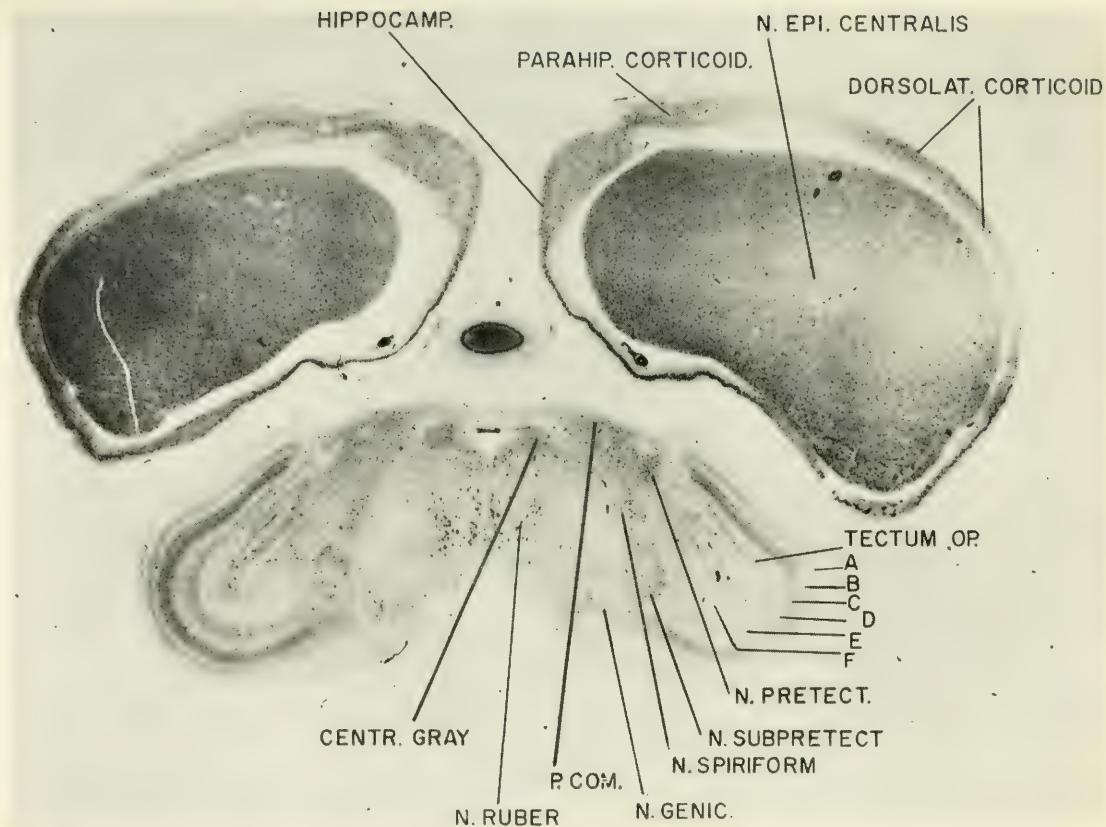


Fig. 10. Serial section #1201. Cresyl Violet stain, magnification X 5.0.

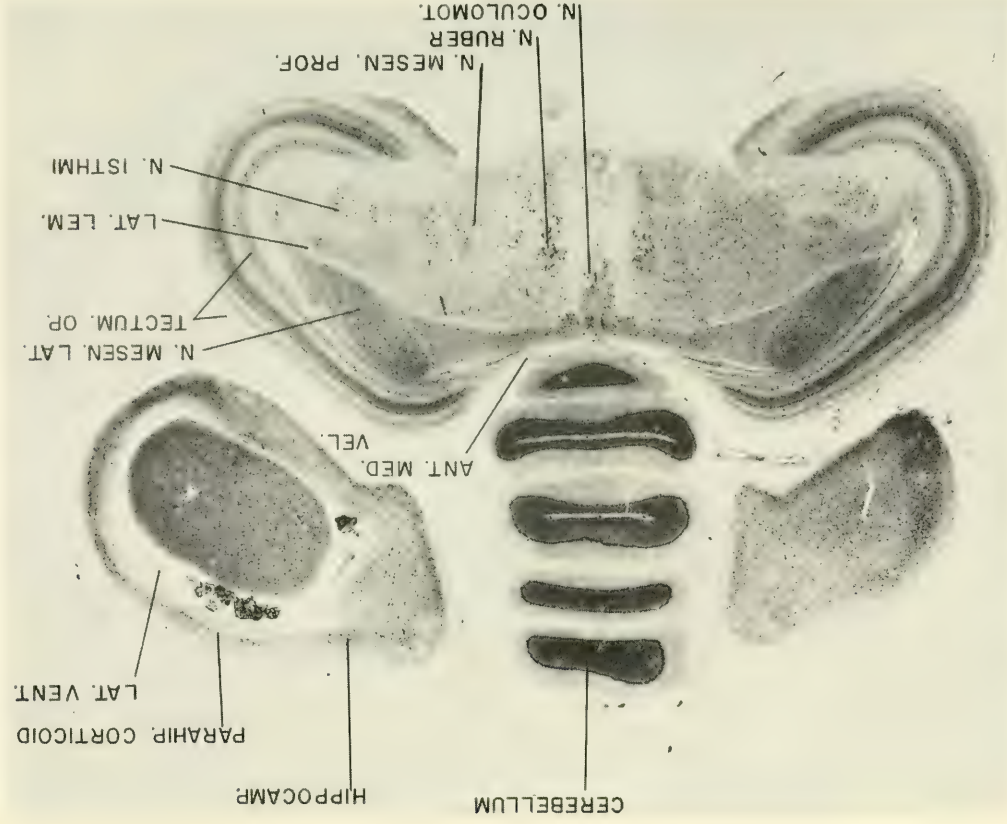


Fig. 11. Serial section #1301. Cresyl Violet stain, magnification X 5.0.

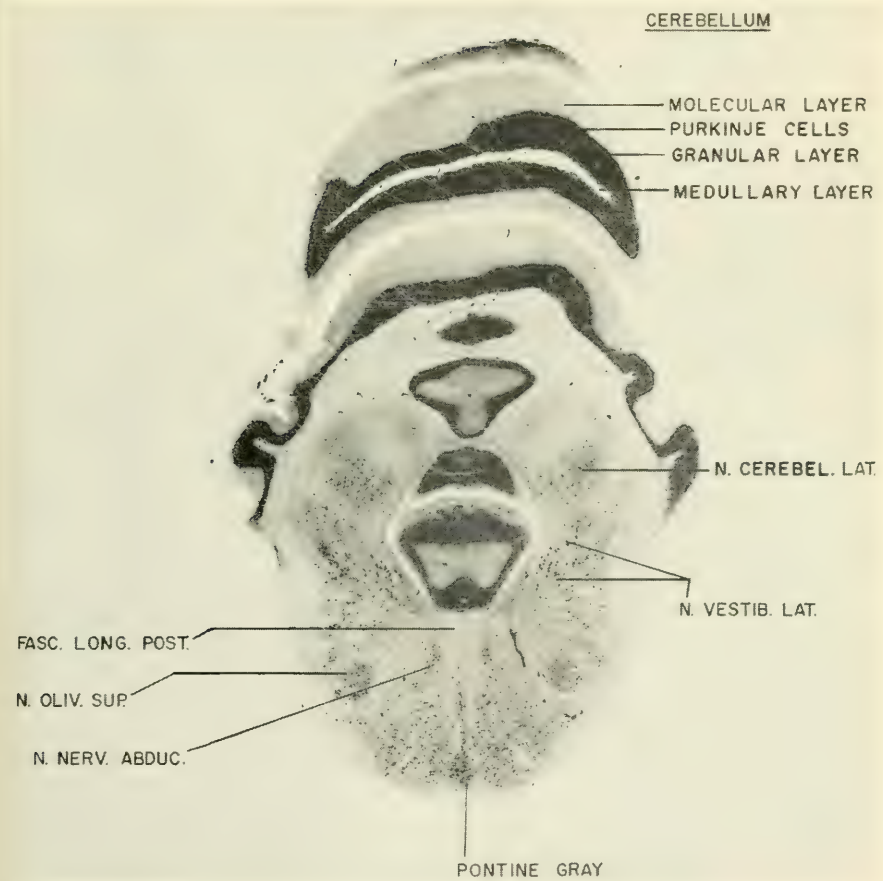


Fig. 12. Serial section #1681. Cresyl Violet stain, magnification X 5.0.